PRACTICAL DIAGNOSIS AND NATURAL HISTORY OF TWO SIBLING SALT MARSH-INHABITING PLANTHOPPERS IN THE GENUS *PROKELISIA* (HOMOPTERA: DELPHACIDAE)

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Abstract.—Two salt marsh-inhabiting planthoppers, *Prokelisia marginata* (Van Duzee) and *Prokelisia dolus* (Wilson), have been the subjects of extensive ecological research. In the past these species have been confused taxonomically because they are difficult to differentiate, particularly the females and nymphs. In this report we show that males can be separated on the basis of style shape; the styles of *P. marginata* project dorsally and are caliper shaped while those of *P. dolus* are flared posteriorly and are avicephaliform in shape. Analysis of morphometric data from laboratory-reared isolines as well as field-collected specimens of each species reveals that females and nymphs are separable using frons morphology. The frons of *P. marginata* is proportionally longer and narrower than that of *P. dolus*. Also, macropters have a slightly longer and narrower frons than brachypters regardless of species. Last, we review the natural history, host plant relationships, and population biology of these two congeneric planthoppers.

Planthoppers in the genus *Prokelisia* have been the focus of extensive ecological study. For example, *Prokelisia marginata* (Van Duzee) has been used to study plant-herbivore interactions (Denno, 1977, 1983; Tallamy and Denno, 1979; Vince et al., 1981; Denno et al., 1986), migration and population dynamics (Denno, 1979, 1983, 1985; Denno and Grissell, 1979; Denno et al., 1980; Denno et al., in prep.; Roderick, 1987), parasite-host interactions (Stiling and Strong, 1982a, b), predator-prey relationships (Döbel and Denno, in prep. a, b), life history theory (Denno and Dingle, 1981; Denno and McCloud, 1985, in prep.), biogeography (Rey, 1981), and wing polymorphism (Denno, 1976, 1978; McCoy and Rey,

1981; Strong and Stiling, 1983; Denno et al., 1985; Roderick, 1987).

There are several reasons why these non-pest sapfeeders have received so much scientific attention. First, planthoppers in the genus *Prokelisia* are extremely abundant on mid-Atlantic coast salt marshes. They comprise 95–99% of all herbivores sampled on their host grass, *Spartina alterniflora* Loisel (Poaceae) (Denno, 1976, 1977; Tallamy and Denno, 1979). Second, *Spartina* dominates the vegetation of North American intertidal marshes where it commonly occurs as extensive, pure stands (Adams, 1963; Blum, 1968; Redfield, 1972; Duncan, 1974). These relatively simple, naturally occurring monocultures are attractive for studying

plant-herbivore interactions in the absence of mixed vegetational effects. Third, these planthoppers exhibit wing dimorphism; there are fully winged macropterous adults and flightless brachypterous adults, allowing for the easy visual identification of migratory and sedentary forms for population studies (Denno, 1976; Denno and Grissell, 1979; Wilson, 1982; Denno et al., 1985). Fourth, intertidal marshes export minerals and organic nutrients and, in doing so, serve as nursery grounds for commercially important coastal fish and shellfish (McHugh, 1966; Gosselink et al., 1973). Thus, it is important to determine if herbivores such as planthoppers significantly reduce *Spartina* production and influence the energetics of the system. Last, the study of planthoppers in the genus *Prokelisia* takes on added significance because some species are ecologically very similar to pest planthoppers like *Nilaparvata lugens* (Stål.), a major threat to rice production in Asia (Brady, 1979; Kisimoto, 1981; Heinrichs et al., 1982; Kenmore et al., 1984; Wilson and Claridge, 1985).

Due to the widespread interest in these planthoppers as subjects for ecological research, it is especially important to identify them accurately. Thus, the primary objective of this report is to elaborate on biosystematics, provide field identification characters, and update the natural history and host plant relationships for the two congeneric salt marsh-inhabiting planthoppers, *P. marginata* and *P. dolus*. The diagnosis of these two species is particularly timely because *P. dolus* is a recently described species (Wilson, 1982), which has been confused with *P. marginata* in the past, and females and nymphs in particular are difficult to identify.

METHODS

To obtain pure laboratory cultures of *P. marginata* and *P. dolus* for genitalic and morphometric analysis, we collected adults of both species from short-form *S. alterniflora* meadows on June 26, 1986 at Tuck-

erton, Ocean County, New Jersey. Isolines for each species were established by transferring two males and one female onto a seedling of *S. alterniflora* enclosed in a plastic tube cage (see Denno et al., 1985, 1986 for details on *Spartina* culture and cage design). Thirty isolines were set up for each species in the laboratory. Oviposition and development occurred and after five weeks F_1 adults began to emerge. The genitalia of all emerging male offspring were examined to verify the purity of the lines. Male and female offspring of 26 successful *P. marginata* isolines and 21 *P. dolus* isolines were preserved in 70% ethanol for electron microscopy and morphometric analysis.

Scanning electron micrographs were taken of the heads (frontal view) and male genitalia (posterior and lateral views) of *P. marginata* and *P. dolus*. We examined both macropters and brachypters of each species from New Jersey and Florida (Gulf) populations. Specimens were dissected, mounted on metal stubs, and coated with carbon followed by gold-palladium. They were photographed at 10 Kv in a Cambridge 100 Stereoscan microscope.

Wilson (1982) reported that the frons of *P. marginata* was generally longer and narrower than that of *P. dolus*. To quantify this observation, frons measurements for macropters and brachypters of both species were made under a stereomicroscope fitted with a filar ocular micrometer. Specimens were oriented so that the plane of the frons was parallel to that of the microscope stage. Frons length was determined by measuring the distance between the frontoclypeal suture and the vertex. Frons width was determined by measuring its widest point. Frons metrics were expressed as a ratio of frons length to width. From the isolines, approximately twenty adults of each sex and wing form and ten nymphs were measured for both species. To determine differences in frons proportion between species, wing forms and sexes, data were examined using analysis of variance (ANOVA, General Linear Model; SAS Institute, 1982). To deter-
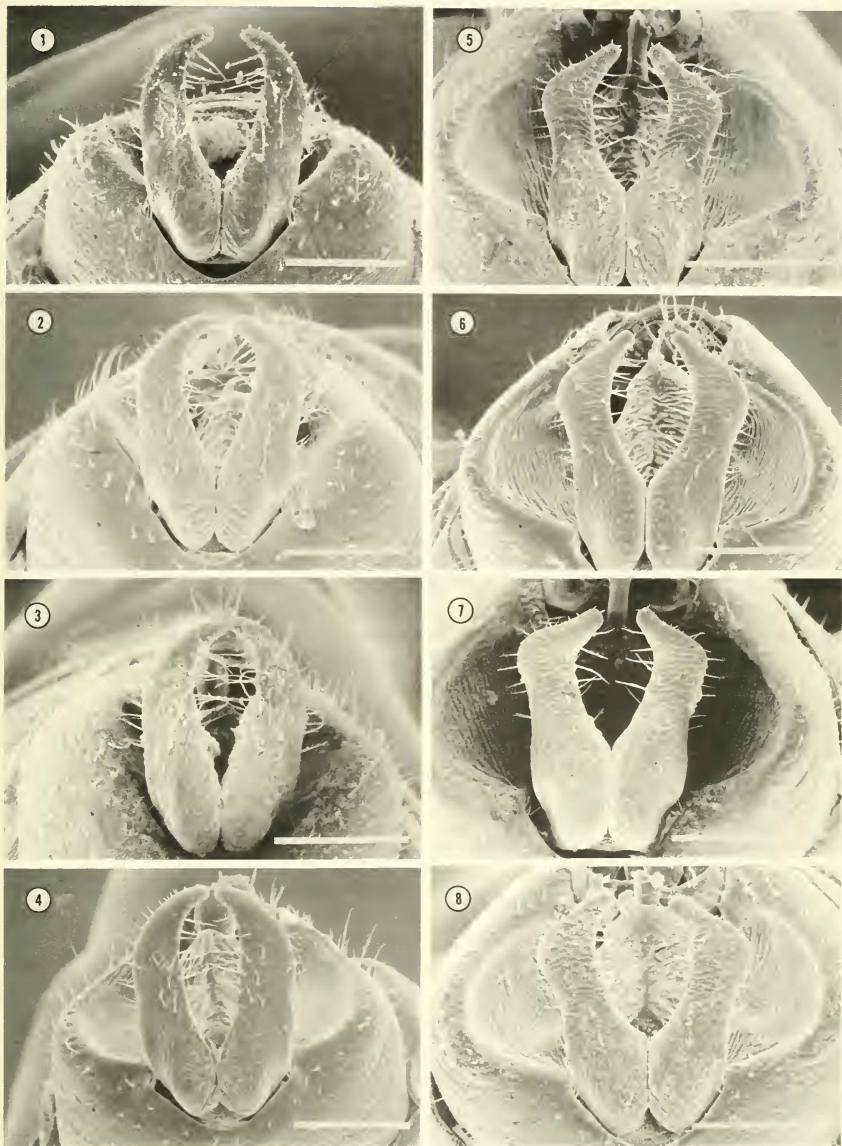
Figs. 1–8. Posterior view of the genital capsule of male *Prokelisia marginata* (1–4) and *P. dolus* (5–8). Macropter, New Jersey (1 and 5); Macropter, Florida (2 and 6); Brachypter, New Jersey (3 and 7); Brachypter, Florida (4 and 8). Note the caliper shape of the styles of *P. marginata* and the avicephaliform shape of the styles of *P. dolus*. Bars on scanning electron micrographs are 0.1 mm.
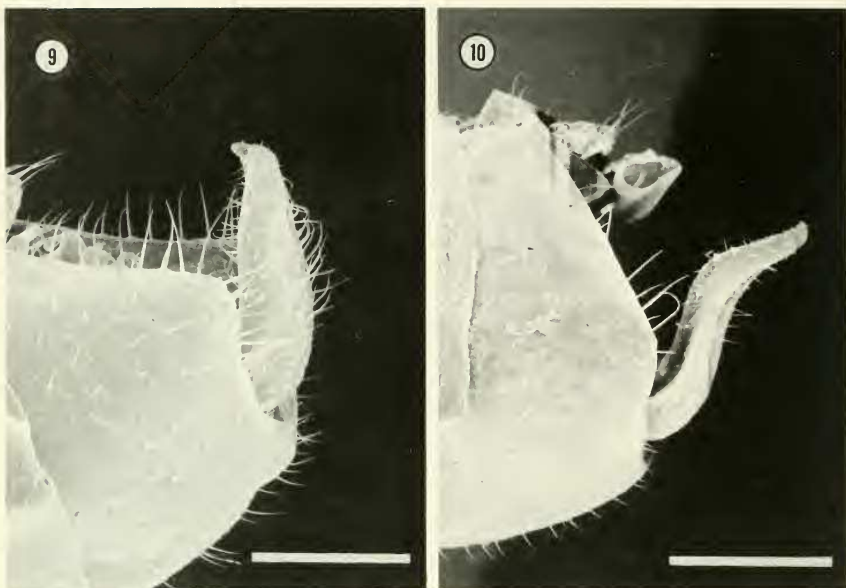
Figs. 9, 10. Lateral view of the styles of male *Prokelisia marginata* (9) and *P. dolus* (10). The styles of *P. marginata* project straight up, while those of *P. dolus* are posteriously flared. Bars on scanning electron micrographs are 0.1 mm.

mine if a skilled technician could accurately identify field-collected material to species, approximately 25 adults of each sex and wing form and 25 fifth instar nymphs for both species were culled from field samples (Tuckerton, N.J.) and sorted to species on the basis of frons shape. Frons measurements were made on these specimens and the resulting frequency distribution was compared to the isoline distribution by ANOVA. The origin (field or isoline) of the populations was entered as a source of variation in the ANOVA model. A significant effect of origin would indicate an inaccurate identification of field-collected specimens.

Results and Discussion

Genitalic distinctness of males.—Although the gross anatomy of *P. marginata* and *P. dolus* is very similar, males are easily separated by the shape of their styles (= claspers) (Wilson, 1982). The styles of *P. marginata* are caliper shaped and taper gradually from the base to the apex (Figs. 1–4). By contrast, the styles of *P. dolus* are avicephaliform and expand distally with angulate outer margins (Figs. 5–8). In lateral view, the styles of *P. marginata* are straight and project dorsally (Fig. 9), whereas those of *P. dolus* are posteriorly flared (Fig. 10). These genitalic characters remain distinct throughout the entire geographic distribution of both species and are not influenced by wing form (see New Jersey-Florida and macropter-brachypter comparisons in Figs. 1–8). In the thousands of male specimens examined, we never observed a genitalic intermediate (Wilson, 1982; this report). Style characters are readily visible under a stereomicroscope, allowing for the rapid iden-
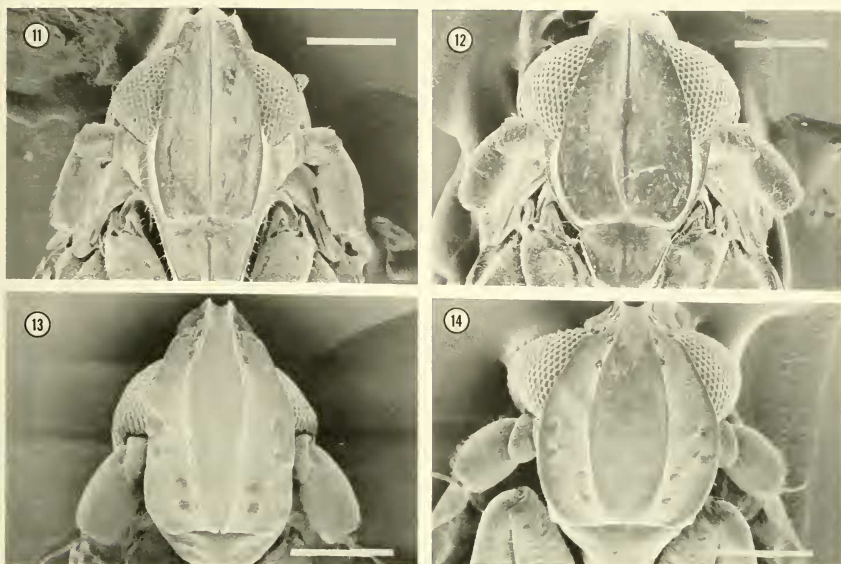
Figs. 11–14. Frontal view of the frons of adult male *Prokelisia marginata* (11) and *P. dolus* (12). Bars on electron micrographs are 0.5 mm. Frontal view of the frons of the fifth instar nymph of *P. marginata* (13) and *P. dolus* (14). Bars on electron micrographs are 0.2 mm.

tification of males in field-collected samples of planthoppers. Additional genitalic differences include the shape and dentition of the aedeagus (Wilson, 1982), slight differences in the shape of the pygofer (Figs. 1–10), and rugose sculpturing over the entire surface of the styles of *P. dolus* (Figs. 1–8). The apical third of styles of *P. marginata* lack rugose sculpturing (Figs. 1–8). These differences, although subtle, are no less so than those observed in the extensively studied *Muellerianella* complex (Drosopoulos, 1977; Booij, 1981).

Morphometric analysis of the frons.— Whereas genitalic characters can be used readily to separate males of *P. marginata* and *P. dolus*, they are not useful for distinguishing between females. Wilson (1982) reports that *P. marginata* generally can be separated from *P. dolus* by its longer and narrower frons (compare Figs. 11 with 12

and 13 with 14). Here we pursue more rigorously the ratio of frons length/frons width as a diagnostic character for identifying females, males and fifth instar nymphs of the two *Prokelisia* species.

The frequency distributions of the frons length/frons width ratio overlap very little between *P. marginata* and *P. dolus* adults from laboratory isolines (Fig. 15 black boxes only). Mean ratios for females of *P. marginata* were 1.810 for brachypters and 1.879 for macropters. Mean frons ratios for *P. dolus* were 1.552 and 1.628 for brachypters and macropters, respectively, documenting the longer and narrower frons of *P. marginata* (Table 1). Analysis of variance on individuals from isolines found a highly significant effect ($P < 0.0001$) of species and wing form on frons ratio (Table 2). Not only is the frons of *P. marginata* longer and narrower than the frons of *P. dolus,* but mac-
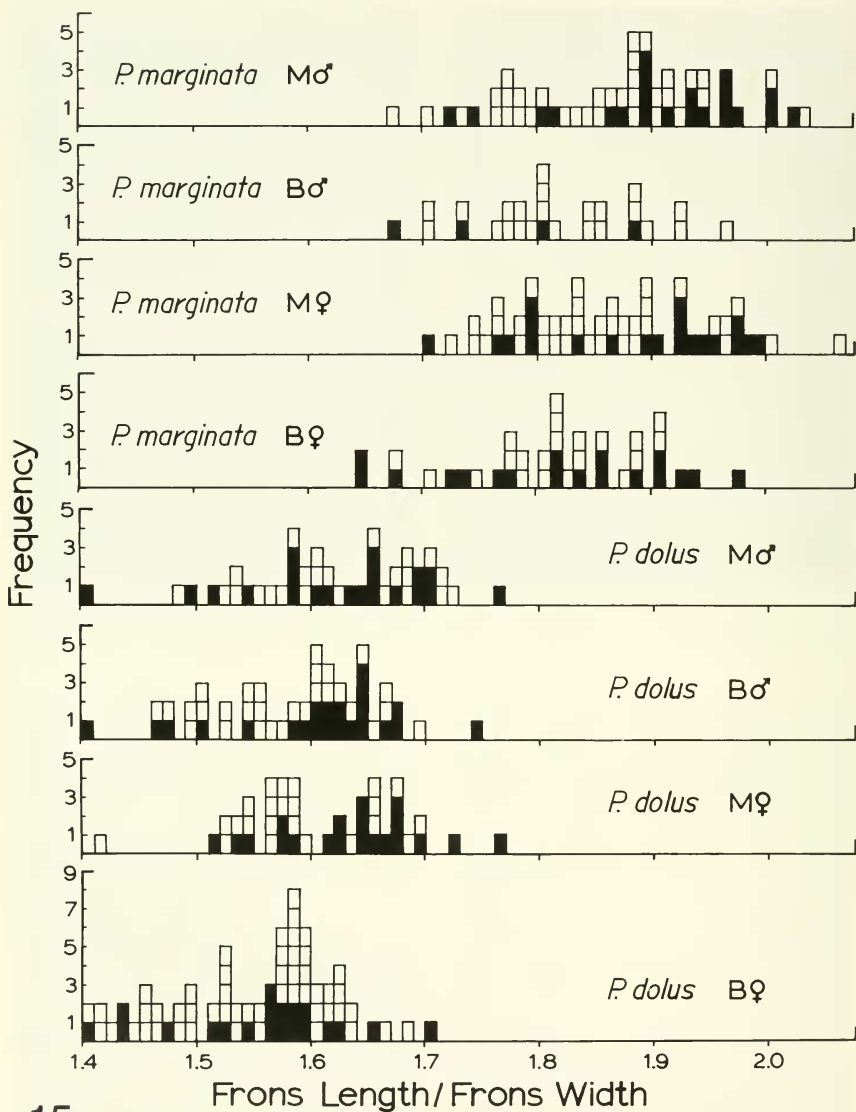
Fig. 15.   Frequency distribution of the ratio of frons length/frons width for the wing forms (M = Macropter, B = Brachypter) and sexes of *Prokelisia marginata* and *P. dolus* from laboratory isolines (black boxes) and field samples collected at Tuckerton, New Jersey (open boxes). ANOVA finds a significant ($P < 0.0001$) effect of species and wing form on frons ratio corroborating the longer and narrower frons of *P. marginata* compared to *P. dolus*, and the slightly longer and narrower frons of macropters compared to brachypters.

Table 1. Mean frons length/frons width ratios with standard errors and sample sizes for the sexes and wing forms of *Prokelisia marginata* and *P. dolus* from laboratory isolines. The higher ratios observed in *P. marginata* document its long, narrow face compared to *P. dolus*.

Species	Sex	Wingform	Mean	SE	n
P. marginata	male	macropter	1.903	.0176	21
P. marginata	male	brachypter	1.772	.0473	4
P. marginata	female	macropter	1.879	.0191	20
P. marginata	female	brachypter	1.810	.0237	18
P. dolus	male	macropter	1.616	.0193	20
P. dolus	male	brachypter	1.597	.0169	22
P. dolus	female	macropter	1.628	.0143	20
P. dolus	female	brachypter	1.552	.0168	20

ropters of both species have a longer and narrower frons than brachypters. Of the explainable variation in adult frons ratio, however, 89% of it is attributable to species effects, while wing form accounts for only 8% (Table 3).

Fifth instar nymphs of *P. marginata* from isolines also have a significantly ($P < 0.0001$) longer and narrower frons (1.441 ± 0.021, $\bar{x} \pm SE$; n = 10) than nymphs of *P. dolus* (1.204 ± 0.017, $\bar{x} \pm SE$; n = 10) (Fig. 16 black boxes only, Table 4). Thus, by using individuals from pure isolines in the laboratory we have determined that most females and fifth instar nymphs can be accurately identified to species by the relative length and width of the frons.

A second objective of our study was to determine if a skilled technician could accurately and quickly sort field-collected adults (particularly females) and nymphs to

species. The rapid and accurate identification of field-collected material is essential for population studies of planthoppers. To determine if this objective was possible, we compared the frequency distribution of the frons length/frons width ratio of individual females originating from isolines in the laboratory (black boxes in Fig. 15) with the frons ratio distribution of field-collected females (open boxes in Fig. 15) that were sorted to species by eye under the microscope. There were no significant effects of origin (isoline vs. eye-sorted field sample) on frons ratio variation, and only species and wing form contributed significantly ($P < 0.0001$) as before (Table 5). These results strongly suggest that a trained technician can accurately sort females of *Prokelisia* to species. This procedure was also conducted on fifth instar nymphs with the same result. They too can be accurately sorted to species by

Table 2. Analysis of variance of the frons length to width ratios of adult *Prokelisia marginata* and *P. dolus* reared from laboratory isolines.

Source of Variation	df	MS	F	P
Species	1	1.5784	233.02	.0001**
Sex	1	.0006	.09	.7698
Species × Sex	1	.0037	.54	.4621
Wingform	1	.1454	21.47	.0001**
Species × Wingform	1	.0183	2.70	.1025
Sex × Wingform	1	.0000	.00	.9495
Species × Sex × Wingform	1	.0231	3.41	.0668
Error	137	.0068		

** Highly significant.

Table 3. Analysis of variance results (% total sums of squares) of the frons length to width ratios of adult *Prokelisia marginata* and *P. dolus* reared from laboratory isolines.

Source of Variation	df	% Total SS
Species	1	58.512**
Sex	1	.022
Species × Sex	1	.137
Wingform	1	5.391**
Species × Wingform	1	.007
Sex × Wingform	1	.000
Species × Sex × Wingform	1	.009
Error	137	34.402

** Highly significant.

Table 4. Analysis of variance of the frons length to width ratios of *Prokelisia marginata* and *P. dolus* nymphs reared from laboratory isolines.

Source of Variation	df	MS	F	P
Species	1	5.7129	72.54	.0001**
Error	19	.0039		

** Highly significant.

eye (compare black boxes with open boxes in Fig. 16).

Because there were no significant effects of population origin on frons ratio variation, we pooled isoline (black boxes in Fig. 15) and field-collected adults (open boxes in Fig. 15) for analysis by ANOVA. Again, only species and wing form contributed significantly ($P < 0.0001$) to the variation in frons ratio (Table 6), accounting for 96% and 3% respectively of the explainable variation. When nymphal data sets (black and open boxes in Fig. 16) were pooled and analyzed, there was a highly significant effect of species on frons ratio ($P < 0.0001$, $F_{1,49} = 146.6$), accounting for 95% of the explainable character variation. The mean frons ratios for the sexes, wingforms and nymphs of *P. marginata* and *P. dolus* are listed in Table 7.

For diagnostic purposes, females with frons ratios of 1.64 or less are unequivocally *P. dolus* and those with ratios of 1.77 and above are *P. marginata*. For brachypterous females the zone of frons ratio overlap lies between 1.64 and 1.71. For macropterous females the zone of uncertainty lies between 1.70 and 1.77 (see Fig. 15). The fifth instar nymphs of *P. dolus* are characterized by having frons ratios of 1.35 or less, while the nymphs of *P. marginata* have ratios of 1.33 or more with a small zone of overlap (1.33–1.35) (see Fig. 16).

From these results we can conclude that the frons of *P. marginata* is proportionally longer and narrower than the frons of *P. dolus* and that macropters have a slightly longer and narrower frons than brachypters regardless of species. The difference in frons proportion between *P. marginata* and *P. dolus* is substantial enough to be recognized without measurement under the microscope by a skilled technician, allowing for the correct identification of most field-collected adults and late instar nymphs.

Distribution and host plants.—Both *P. marginata* and *P. dolus* are widely distributed throughout the coastal salt marshes of North America. *P. marginata* occurs from Massachusetts to Florida on the Atlantic Coast, from Florida to Louisiana along the Gulf Coast, and has been recorded from the isolated Pacific tidal marshes of California (Wilson, 1982). *P. dolus* has a very similar geographic distribution, occurring from New Hampshire to Florida along the Atlantic Coast, from Florida to Texas along the Gulf, and sporadically in the tidal estuaries of southern California (Wilson, 1982).

Throughout their geographic distribution, *P. marginata* and *P. dolus* feed and reproduce primarily on two closely related species of salt marsh cord grasses. Along the Atlantic and Gulf coasts, *S. alterniflora* is by far their predominant host plant (Denno, 1977, 1983, 1985; Denno and Grissell, 1979; Strong and Stiling, 1983), whereas their Pacific host is *S. foliosa* Trin. (Roderick, 1987). Museum specimens often bear erroneous host labels such as "*Spartina patens*" or "*Juncus roemerianus*" (see Wilson, 1982).

Table 5. Analysis of variance of the frons length to width ratios of *Prokelisia marginata* and *P. dolus* females originating from isoline cultures in the laboratory and field populations at Tuckerton, New Jersey.

Source of Variation	df	MS	F	P
Species	1	3.2182	574.65	.0001**
Origin	1	.0151	2.70	.1019
Species × Origin	1	.0024	.43	.5112
Wingform	1	.1449	25.87	.0001**
Species × Wingform	1	.0000	.00	.9585
Origin × Wingform	1	.0138	2.47	.1176
Species × Origin × Wingform	1	.0003	.06	.8065
Error	203	.0056		

** Highly significant.

These grasses and rushes are also salt marsh halophytes, and, although migrating or stranded *Prokelisia* may be collected from them, they do not serve as hosts for reproduction and development in the mid-Atlantic states (Denno and Grissell, 1979; Denno et al., 1985; Denno, unpub. data). McCoy and Rey (1981) report that immatures and brachypters of *P. marginata* were common in a *Spartina patens-Distichlis spicata* meadow on a Gulf Coast marsh in Florida. They reason that while *S. alterniflora* serves as the primary host for *P. marginata* in most of western Florida, the grass was rare at their study site, which perhaps provided the opportunity for the planthopper to expand its host range. While phytophagous insects certainly do adapt to new species of hosts (Bush, 1975; Bush and Diehl, 1982; Gould, 1983; Mitter and Futuyma, 1983; Tabashnik, 1983), host shifting must be construed as a rare situation for these planthoppers, given the overwhelming amount of evidence favoring *S. alterniflora* and *S. foliosa* as primary hosts. Furthermore, *P. marginata* and *P. dolus* have been raised successfully through several generations in the laboratory only on seedlings, transplants, or ramets of *S. alterniflora* and *S. foliosa* (this report; Roderick, 1987).

Natural history and population biology.—As noted above, *P. marginata* and *P. dolus* are the most abundant herbivorous insects on mid-Atlantic marshes, with population densities of both species exceeding 1000 adults/m^2 in *Spartina alterniflora* (Denno, 1976, 1977; Tallamy and Denno, 1979; Denno et al., 1985). Along the Gulf Coast the average density of *P. marginata* is at least one order of magnitude lower than it is on mid-Atlantic marshes (Denno, 1983; Strong and Stiling, 1983).

Table 6. Analysis of variance of the frons length to width ratios of adult *Prokelisia marginata* and *P. dolus* reared from isolines in the laboratory and collected in the field at Tuckerton, New Jersey.

Source of Variation	df	MS	F	P
Species	1	5.7129	986.31	.0001**
Sex	1	.0188	3.25	.0722
Species × Sex	1	.0091	1.57	.2107
Wingform	1	.2203	38.04	.0001**
Species × Wingform	1	.0027	.46	.4966
Sex × Wingform	1	.0014	.25	.6171
Species × Sex × Wingform	1	.0055	.95	.3313
Error	381	.0058		

** Highly significant.
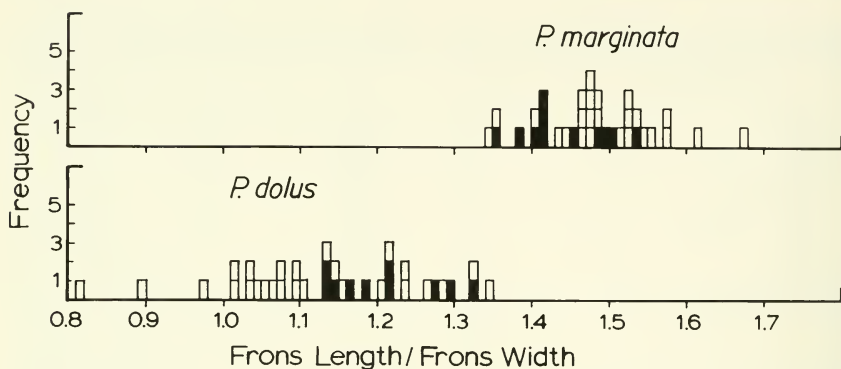
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Fig. 16.   Frequency distribution of the ratio of frons length/frons width for the fifth instar nymphs of *Prokelisia marginata* and *P. dolus* from laboratory isolines (black boxes) and field samples collected at Tuckerton, New Jersey (open boxes). ANOVA finds a significant (*P* < 0.0001) effect of species on frons ratio corroborating the longer and narrower frons of *P. marginata* compared to *P. dolus*.
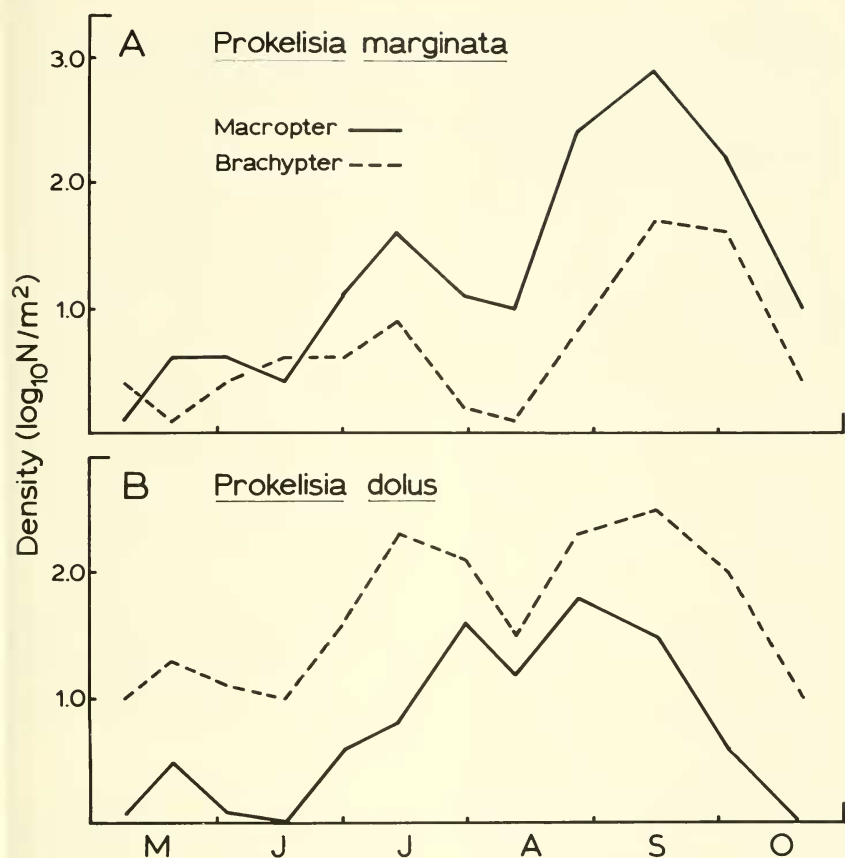
In New Jersey both *P. marginata* and *P. dolus* are at least trivoltine, and perhaps quadrivoltine in warm years, with peaks of adult abundance during May, July, and September (Fig. 17). Adults are usually absent from the marsh from November through March. On the Gulf Coast of Florida, adults of *P. marginata* are present all year and reproduction is probably continuous, result-

ing in six or more generations per year (Denno, 1983; Strong and Stiling, 1983).

The five nymphal instars and adults of both species feed on the phloem sap of their grass hosts. Planthoppers feed mostly from the upper surface of leaf blades and avoid stems and sheaths except at very high densities. Females insert their eggs with swordlike ovipositors between the ridges on the

Table 7.   Means frons length/frons width ratios with standard errors and sample sizes for the sexes, wing forms and nymphs of *Prokelisia marginata* and *P. dolus*. Descriptive statistics based on pooled laboratory-reared and field-collected individuals from Tuckerton, New Jersey.

Species	Sex	Wingform	Mean	SE	n
Adults					
P. marginata	male	macropter	1.871	.0113	56
P. marginata	male	brachypter	1.813	.0142	27
P. marginata	female	macropter	1.863	.0107	57
P. marginata	female	brachypter	1.812	.0127	40
P. dolus	male	macropter	1.617	.0017	44
P. dolus	male	brachypter	1.584	.0098	51
P. dolus	female	macropter	1.604	.0102	43
P. dolus	female	brachypter	1.548	.0085	71
Nymphs					
P. marginata			1.475	.0122	36
P. dolus			1.142	.0211	35

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Fig. 17. Seasonal distribution of the female wing forms of *Prokelisia marginata* and *P. dolus* collected in a *Spartina alterniflora* meadow at Tuckerton, New Jersey during 1982. Notice that the population of *P. marginata* is composed mostly (>80%) of macropters, while brachyptery predominates (>70%) in the *P. dolus* population.

upper surface of blades. In mid-Atlantic populations, active nymphs overwinter in litter or rolled dead leaves of standing vegetation (Denno, 1977). Tallamy and Denno (1979) reported that if litter is removed in autumn, significantly smaller populations occur the following season, suggesting that litter is a critical resource for winter survival.

The most striking ecological difference between *P. marginata* and *P. dolus* is the wing form composition of populations along the Atlantic coast where both species are so abundant. Populations of *P. marginata* are

composed of >80% macropters, while the proportion is reversed in *P. dolus* with macroptery rarely exceeding 20% (Wilson, 1982; Denno, 1985; Denno et al., 1985). The discrepancy in wing form composition of populations reflects a major difference in mobility between the two species. *P. marginata* is a migratory species on the Atlantic coast, undergoing annual interhabitat movements between overwintering habitats on the high marsh (short-form *Spartina*) and better summer sites for development on the low marsh (tall-form *Spartina*) (Denno and Grissell, 1979; Denno, 1983, 1985; Denno et al., 1985). By moving to low marsh sites during the summer, immigrant planthoppers encounter a much more nutritious host plant than they would had they remained on the high marsh. For *P. marginata*, feeding on a more nutritious host results in larger females with increased fecundity (Denno and McCloud, 1985; Denno et al., 1986). Denno et al. (1986) argue that the contrast in *Spartina* nutrition between high and low marsh habitats as well as differential winter survival in these habitats have been major selective forces behind the evolution of migration in *P. marginata*. By contrast, *P. dolus* is a very sedentary species, remaining mostly on the high marsh in short-form *Spartina* throughout the entire year (Denno et al., 1985; Denno et al., in prep.). Currently, far less is known about the population dynamics of *P. dolus*.

Along the Gulf Coast, populations of both species are composed on average of 90% brachypters, a situation very different from that along most of the Atlantic coast (Denno and Grissell, 1979; McCoy and Rey, 1981; Wilson, 1982; Strong and Stiling, 1983; Denno, 1985). Explanations for the high levels of brachyptery in Gulf Coast populations of *P. marginata* include the persistence and homogeneity of *Spartina* stands (Denno and Grissell, 1979; Denno, 1983, 1985), the isolation of *Spartina* patches (McCoy and Rey, 1981), and the selective

loss of dispersing macropters from islets of *Spartina* (Strong and Stiling, 1983).

For *Prokelisia marginata* and *P. dolus* there appears to be a strong environmental component involved in wing form determination, particularly for females (Denno et al., 1985; Denno, unpub. data; Roderick, 1987). Various environmental conditions experienced during nymphal development act as cues, triggering a developmental switch that selects one of several alternative morphogenic pathways (Lees, 1961, 1966; Mochida, 1973; Denno et al., 1985). Of the cues investigated, crowding has by far the most significant effect on wing form, although host plant nutrition and temperature have an influence as well (Denno et al., 1985; Denno, unpub. data). At high densities on poor quality hosts most adults molt to macropters, enabling them to escape deteriorating host plants. However, the threshold density that triggers the production of macropters is much lower for *P. marginata* than *P. dolus*. This provides a proximate explanation for the much higher levels of macroptery in *P. marginata* compared to *P. dolus* populations that occur in the mid-Atlantic states (Denno, 1985; unpub. data).

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